

# Dispersion relations to oscillatory reaction-diffusion systems with the self-consistent flow

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## Abstract

Dispersion curves to a oscillatory reaction-diffusion system with the self-consistent flow have obtained by means of numerical calculations. The flow modulates the shape of dispersion curves and characteristics of traveling waves. The point of inflection which separates the dispersion curves into two branches corresponding to trigger and phase waves, moves according to the value of the advection constant. The dynamics of phase wave in reaction-diffusion-advection equations has been studied by limit cycle perturbations. The dispersion relation obtained from the phase equation shows that the competition between diffusion and advection constants modulates the oscillation frequency from the bulk oscillation in the long-wave dynamics. Such a competition implies that phase waves with the flow have a wider variety of dynamics than waves without the flow.

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## I. INTRODUCTION

In biological systems of cell population, taxis induces cooperative movement of cells or the flow of cellular mass. Cells behave according to chemical and physiological signals given by themselves. Two well-known pattern formations for population dynamics of cells are the aggregation of cellular slime molds and the branching growth of bacterial colonies. Slime mould cells secrete signaling chemicals responding to extracellular chemicals, and move towards increasing some chemical concentration. They aggregate to centers of the wave pattern of chemicals with dendritic streaming lines and eventually form slugs [1,2,3]. Morphology of bacterial colonies depends on agar concentration and nutrient level. Bacteria are swimming toward high concentration of nutrients, and form various colonial patterns as concentric rings and dendritic branchings [4,5,6]. Mechanisms of these pattern formations have been modeled by taxis equations or reaction-diffusion systems with the cellular flow.

For one of protozoan myxomycete, the *Physarum* plasmodium, which is a unicellular organism, a reaction-diffusion-flow model is presented in relation to control mechanism of amoeboid movements. The flow of endoplasm and chemicals induced by protoplasmic streaming in *Physarum* plays an important role in individual behavior under a large plasmodium state. It is not difficult to look for reaction, diffusion and flow couplings in various biological process, more and more. The self-consistent flow as above is realized by biological active process, and is a different character from physico-chemical ones. Effects of the self-consistent flow on simple reaction-diffusion systems are to be clarified in order to study a mechanism of functional self-organization of multicellular systems.

In the present article, we discuss basic effects of the flow on oscillatory phenomena in a reaction-diffusion system with the self-consistent flow. Although we dealt with a model for the *Physarum* plasmodium, it is expected that the results obtained here are applicable to other biological systems with the flow. We carry out numerical calculation of the dispersion relation in the system, and show effects of the flow on traveling plane waves. Then we derive the dynamics of phase waves from reaction-diffusion-advection equations in general form

by means of limit cycle perturbations. In the coefficient of the gradients of the phase, the advection terms compete with diffusion terms.

## II. MODEL EQUATIONS FOR THE PLASMODIUM

The plasmodium of *Physarum* has a cytoplasmic cortex (ectoplasm) filled with endoplasm. The ectoplasm shows contractile oscillation everywhere within the organism [7,8,9], and the contraction causes intracellular streaming of the endoplasm [10]. The contraction-relaxation behavior is regulated by metabolic cycles of chemical oscillators [11,12]. Metabolic chemicals transported by endoplasmic streaming, affect chemical oscillators [13,14,15].

A model of contractile and motile dynamics of the *Physarum* plasmodium is represented by conservation of the cytoplasmic mass and reaction-diffusion system of metabolic elements with endoplasmic streaming [16,17]. Under some assumptions, oscillatory dynamics in the plasmodium is governed by the following reaction-diffusion equations with advection terms:

$$\frac{\partial \mathbf{u}}{\partial t} + M \vec{\nabla} \mathbf{u} \cdot \vec{\nabla} \mathbf{u} = \mathbf{f}(\mathbf{u}) + D \vec{\nabla}^2 \mathbf{u}, \quad (1)$$

where  $\mathbf{u}$  is a  $N$ -component vector of reaction species which are separated into two types of metabolic elements, free chemicals and non-free ones. While the former is transported by the protoplasmic streaming, the latter is bound or stored at some cytoplasmic structure. Reaction kinetics  $\mathbf{f}$  denotes the metabolic oscillation which emerges from the coupling of two types of reaction elements mentioned above, and the system is assumed to have a limit cycle orbit. The quantity  $D$  is a diagonal matrix of diffusion constants. A tensor  $M$  represents advection coefficients, here  $M \vec{\nabla} \mathbf{u}$  is a flow vector for each reaction component. This system has a generic form of reaction-diffusion equations with the self-consistent flow, and we derive the phase dynamics from eq. 1 in section IV.

In our numerical calculations, we use a more simple two-variable model [17]:

$$\begin{aligned} \frac{\partial u}{\partial t} + \vec{w} \cdot \vec{\nabla} &= f(u, v) + D \vec{\nabla}^2 u, \\ \frac{\partial v}{\partial t} &= g(u, v), \end{aligned} \quad (2)$$

where  $u$  and  $v$  are the concentrations of a free chemical substance and a bound/stored one, respectively. We adopt the Schnackenberg's tri-molecular two species model for reaction kinetics of chemicals [18],

$$f(u, v) = a - u + u^2v, \quad g(u, v) = b - u^2v, \quad (3)$$

here  $a$  and  $b$  are positive constants. In the spatially homogeneous conditions ( $D = 0$  and  $\vec{w} = \vec{0}$ ), the system has a stable limit cycle as shown in Fig. 1 for  $b - a > (a + b)^3$ . The quantity  $D$  is the diffusion constant of the free chemical  $u$ . The velocity of the endoplasmic flow  $\vec{w}$  is determined by the concentration of the metabolic chemical as

$$\vec{w} = q\vec{\nabla}u, \quad (4)$$

and thus the flow is self-consistent. Here  $q$  depends on the permeability and the mechanism of intracellular pressure. In the following calculation,  $q$  is assumed to be constant.

### III. DISPERSION RELATION

The numerical calculations were carried out for eq. 2 on a ring, that is a one-dimensional region with periodic boundary conditions. Using the limit cycle, we initiate a pulse traveling on the ring, and solve eq. 2 until the solution becomes periodic in time. After we measured the rotating period of the traveling pulse on the ring, we repeat the calculation for rings of different lengths. As above, the dispersion relation has been obtained for periodic wave trains with the stable propagation.

In the measurements, parameters have been set as  $a = 0.1$ ,  $b = 0.5$ , and  $D = 1.0$ . We have used the explicit Euler's method for reaction terms, upwind differencing method for advection terms, and the implicit method for diffusion terms. The data have been recorded for waves in stationary propagation.

Dispersion curves in the reaction-diffusion-advection system 2 are shown in Fig. 2 (wave number vs frequency) and Fig. 3 (period vs velocity) for various values of the advection

constant  $q$ . Variations in the self-consistent flow make the propagation of plane waves quite changed. The inflection point which separates two branches corresponding to trigger waves and phase waves [19,20], moves according to the flow. It is the point that the variation of propagating behavior depends on the wave length. The other point is that the sign of  $q$  gives different effects on waves in propagation features.

For the positive value of  $q$ , the oscillation frequency  $\omega$  of phase waves gets slightly greater, while that of trigger waves becomes smaller. Hence, phase waves travel a longer way for the greater value of  $q$  even if they have the same frequency. Such a case of positive  $q$  corresponds to the phenomena of phase waves in the plasmodium, when we regard the reaction kinetics of eq. 3 as the oscillation of some metabolic element like  $\text{Ca}^{2+}$ . The flow make the plasmodium communicate local information to the wide area in the cell with phase waves.

When the advection constant  $q$  is negative, the opposite situation to the case of positive  $q$  arises. Furthermore, we find out the steep rise of the frequency in Fig. 2. Such steepness denotes the sharp transition from phase waves to trigger waves with increasing dimensions of the propagating media.

#### IV. PHASE DYNAMICS

In this section, we show that the effect of the flow comes out through the coefficient of the nonlinear term in phase dynamics for reaction-diffusion-advection systems. By means of limit cycle perturbations, the dynamics of phase waves in ordinary reaction-diffusion systems for oscillatory media are described by the Burgers equation [21,22]. We adopt the similar method to oscillatory reaction-diffusion equations with advection terms introduced in section II.

We assume that the limit cycle of eq. 1 has the frequency  $\omega_0$ . Then a solution of homogeneous oscillation is

$$\begin{aligned} \mathbf{u} &= \mathbf{u}_0(\tau), \quad \tau = \omega_0 t, \quad \text{where} \\ \omega_0 \mathbf{u}_0' &= \mathbf{f}(\mathbf{u}_0), \quad \text{and} \quad \mathbf{u}_0(\tau + 2\pi) = \mathbf{u}_0(\tau). \end{aligned}$$

Since the system 1 is invariant under the time translation,  $\mathbf{u}_0(\tau + \psi)$  ( $\psi$  is an arbitrary constant) is also a solution of eq. 1.

Let us consider the dynamics of phase waves in eq. 1 when the advection and diffusion terms are small. We introduce multiple scales and asymptotic expansions,

$$\begin{aligned}\vec{R} &= \sqrt{\epsilon}\vec{r}, \quad \tau = \omega_0 t, \quad T = \epsilon t, \\ \mathbf{u} &= \mathbf{u}_0(\tau + \psi) + \epsilon \mathbf{u} + \dots,\end{aligned}\tag{5}$$

where  $\epsilon$  is a small parameter and  $\psi = \psi(\vec{R}, T)$ . Substitution of eq. 5 into eq. 1 yields perturbation equations for each order in  $\epsilon$ :

$$\begin{aligned}\omega_0 \frac{\partial \mathbf{u}_0}{\partial \tau} &= \mathbf{f}(\mathbf{u}_0), \\ L \mathbf{u}_j &= \mathbf{b}_j, \quad L = \omega_0 \frac{\partial}{\partial \tau} - \frac{\partial \mathbf{f}}{\partial \mathbf{u}}(\mathbf{u}_0),\end{aligned}\tag{6}$$

here  $j = 1, 2, \dots$ , and  $\mathbf{b}_j$  denotes the inhomogeneous term of the  $j$ th order equation. For the first order equation in eq. 6, the inhomogeneous term is

$$\begin{aligned}\mathbf{b}_1 &= -\frac{\partial \mathbf{u}_0}{\partial T} - M \vec{\nabla}_R \mathbf{u}_0 \cdot \vec{\nabla}_R \mathbf{u}_0 + D \vec{\nabla}_R^2 \mathbf{u}_0 \\ &= -\mathbf{u}'_0 \frac{\partial \psi}{\partial T} - M \mathbf{u}'_0 \mathbf{u}'_0 |\vec{\nabla}_R \psi|^2 \\ &\quad + D \mathbf{u}''_0 |\vec{\nabla}_R \psi|^2 + D \mathbf{u}'_0 \vec{\nabla}_R^2 \psi,\end{aligned}$$

where  $\vec{\nabla}_R$  is the nabla operator in respect to scaled coordinates  $\vec{R}$ . Thus the solvability condition for  $\mathbf{u}_1$  gives the dynamics of phase waves:

$$\frac{\partial \psi}{\partial T} = c_1 \vec{\nabla}_R^2 \psi + c_2 |\vec{\nabla}_R \psi|^2.\tag{7}$$

If we use a new dependent variable  $\vec{V} \equiv \vec{\nabla}_R \psi$ , then it satisfies the Burgers equation. The coefficients  $c_1$  and  $c_2$  are obtained from the relations,

$$\begin{aligned}c_j &= \langle \mathbf{v}^\dagger, \mathbf{v}_j \rangle / \langle \mathbf{v}^\dagger, \mathbf{u}_0 \rangle, \\ \mathbf{v}_1 &= D \mathbf{u}'_0, \quad \mathbf{v}_2 = D \mathbf{u}''_0 - M \mathbf{u}'_0 \mathbf{u}'_0,\end{aligned}$$

here  $\langle \mathbf{v}^\dagger, \mathbf{v} \rangle \equiv \int_0^{2\pi} d\psi (\mathbf{v}^\dagger, \mathbf{v})$  and  $\mathbf{v}^\dagger$  is the nontrivial periodic solution to the adjoint differential equation of  $L\mathbf{v} = \mathbf{0}$ . Equation 7 describes slow and slight modulation of the homogeneous oscillation with the frequency  $\omega_0$  by the phase  $\psi$ . We note that the coefficient of the nonlinear term,  $c_2$ , show competition between diffusion and advection.

When we use the quantity  $\phi = \omega_0 t + \psi$ , eq. 7 becomes

$$\frac{\partial \phi}{\partial t} = \omega_0 + c_1 \vec{\nabla}^2 \phi + c_2 |\vec{\nabla} \phi|^2. \quad (8)$$

The dispersion relation is thus estimated from the phase equation 8 through the wave characteristics  $\omega = \partial \phi / \partial t$  and  $\vec{k} = \vec{\nabla} \phi$  as [19]

$$\omega = \omega_0 + c_2 k^2 + \dots, \quad k = |\vec{k}|. \quad (9)$$

Since the scaling of coordinates in the perturbation expansions 5 means spatially slight modulation,  $k = O(\sqrt{\epsilon})$ , eq. 9 is the Taylor expansion for the dispersion curve,  $\omega = \omega(k)$  in the vicinity of  $k = 0$ . Thus, the coefficient of nonlinear term in eq. 8 is  $c_2 = \omega''(0)/2$ . Here eq. 9 has no linear term in  $k$  because of the reflectional symmetry in space of eq. 1. As mentioned above,  $c_2$  depends on advection constants as well as diffusion constants, and hence  $c_2$  can take the value of a wide range.

We point out that the dispersion relation 9 is only applicable to some of periodic waves with stationary traveling. It is not adopted to waves with non-uniform phase gradients [20]. In such a case, we need to use the phase equation 8, or analyze eq. 1 directly.

## V. DISCUSSION

By means of numerical calculations for eq. 2, it has been shown that the flow make remarkable differences in the dispersion curves or propagation of phase waves. To elucidate such differences induced by the flow, we consider the spatial scale. The two-component system 2 has the diffusion term only in the free element. Thus, without advection term, the variation of the diffusion constant is canceled by the scaling of spatial coordinates. In

contrast, such a cancellation is impossible with the advection term because the advection coefficient is independent of the diffusion constant.

The deformation of the dispersion curves with the flow term has been shown for the branch of phase waves by the phase equation derived from eq. 1. Furthermore, we have found out another phenomenon of phase wave mentioned below.

Advection coefficients govern the coefficient  $c_2$  of the quadratic term in the wave number  $k$  to the dispersion relation 9. The coefficient  $c_2$  is given by the addition of two parts which stem from the diffusion and advection terms, respectively. Thus, the competition between the diffusion and advection constants governs the value of  $c_2$ . The variation of  $c_2$  gives a quadratic change in the frequency of long waves. This result elucidates the branch of phase waves ( $k \sim 0$ ) for the dispersion curves obtained numerically in section III.

Varying the advection constants, we can take  $c_2$  negative. Such a situation seems to be impossible for simple reaction-diffusion equations without the advection terms. The dispersion curve is convex for  $c_2 < 0$ , and hence  $\omega = 0$  at some wave number. This means that the phase wave is frozen and stationary. It sounds strange, and we need to study these waves in detail. One of such a system is the  $\lambda$ - $\omega$  system with advection terms of phase gradients [23].

When the coefficient  $c_2$  becomes sufficiently small, it may be possible to derive other types of phase equations by introducing different scaling of independent variables from ones used in the present analysis. Furthermore we need to study waves with relaxation oscillations to know the characteristics of trigger waves with the flow, because the phase equation is satisfied only in the region of the phase-wave branch.

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## REFERENCES

- [1] J. T. Bonner, *Life Cycles* (Princeton University Press, Princeton, 1994)
- [2] P. N. Devreotes, *Science* **245**, 1054 (1989).
- [3] K. J. Tomchik and P. N. Devreotes, *Science* **212**, 443 (1981).
- [4] E. O. Burdene and H. C. Berg, *Nature* **349**, 630 (1991); **376**, 49 (1995).
- [5] E. Ben-Jacob, A. Tenenbaum, O. Shochet, and O. Avidan, *Physica A* **202**, 1 (1994); I. Golding, Y. Kozlovsky, I. Cohen and E. Ben-Jacob, *Physica A* **260**, 510 (1998).
- [6] K. Kawasaki, A. Mochizuki, M. Matsushita, T. Umeda and N. Shigesada, *J. Theor. Biol.* **188**, 177 (1997); M. Matsushita, J. Wakita, H. Itoh, I. Ràfols, T. Matsuyama, H. Sakaguchi and M. Mimura, *Physica A* **249**, 517 (1998).
- [7] T. Ueda and K. Gotz von Olenhusen, *Exp. Cell Res.* **116**, 55 (1978).
- [8] W. Naib-Majani, W. Stockem and K-E. W. Bottermann, *Eur. J. Cell Biol.* **28**, 103 (1982).
- [9] M. Ishigami, *Cell Motil. Cytoskeleton* **6**, 439 (1986).
- [10] N. Kamiya, *Protoplasmatol.* **8**, 1 (1959).
- [11] A. Grebecki and M. Cieslawska, *Protoplasma* **97**, 365 (1978).
- [12] Z. Baranowski and K-E. W. Bottermann, *Eur. J. Cell Biol.* **27**, 1 (1982).
- [13] Y. Yoshimoto and N. Kamiya, *Protoplasma* **95**, 111 (1978).
- [14] Y. Miyake, M. Yano and H. Shimizu, *Protoplasma* **162**, 175 (1991).
- [15] T. Nakagaki and T. Ueda, *J. Theor. Biol.* **179**, 261 (1996).
- [16] V. A. Teplov, Yu. M. Romanovsky, and O. A. Latushkin, *Biosystems* **24**, 269 (1991); D. A. Pavlov, Yu. M. Romanovskii, and V. A. Teplov, *Biofizika* **41**, 146 (1996) [*Biophysics* **41**, 153 (1996)].

- [17] H. Yamada, T. Nakagaki and M. Ito, Phys. Rev. E **59**, 1009 (1999); T. Nakagaki, H. Yamada and M. Ito, J. Theor. Biol. **197**, 497 (1999).
- [18] J. Schnackenberg, J. Theor. Biol. **81**, 389 (1979); J. D. Murray, *Mathematical Biology* (Springer 1989) p. 156.
- [19] R. R. Aliev, J. Phys. Chem. **98**, 3999 (1994); R. R. Aliev and V. N. Biktashev, J. Phys. Chem. **98**, 9676 (1994).
- [20] A. A. Polezhaev, Physica D **84**, 253 (1995).
- [21] P. Ortoleva and J. Ross, J. Chem. Phys. **58**, 5673 (1973); P. Ortoleva and J. Ross, J. Chem. Phys. **60**, 5090 (1974); P. Ortoleva, J. Chem. Phys. **64**, 1395 (1976).
- [22] Y. Kuramoto and T. Tsuzuki, Prog. Theor. Phys. **54**, 687 (1975); Y. Kuramoto and T. Yamada, Prog. Theor. Phys. **56**, 724 (1976).
- [23] H. Yamada and T. Nakagaki, in preparation.

# FIGURES

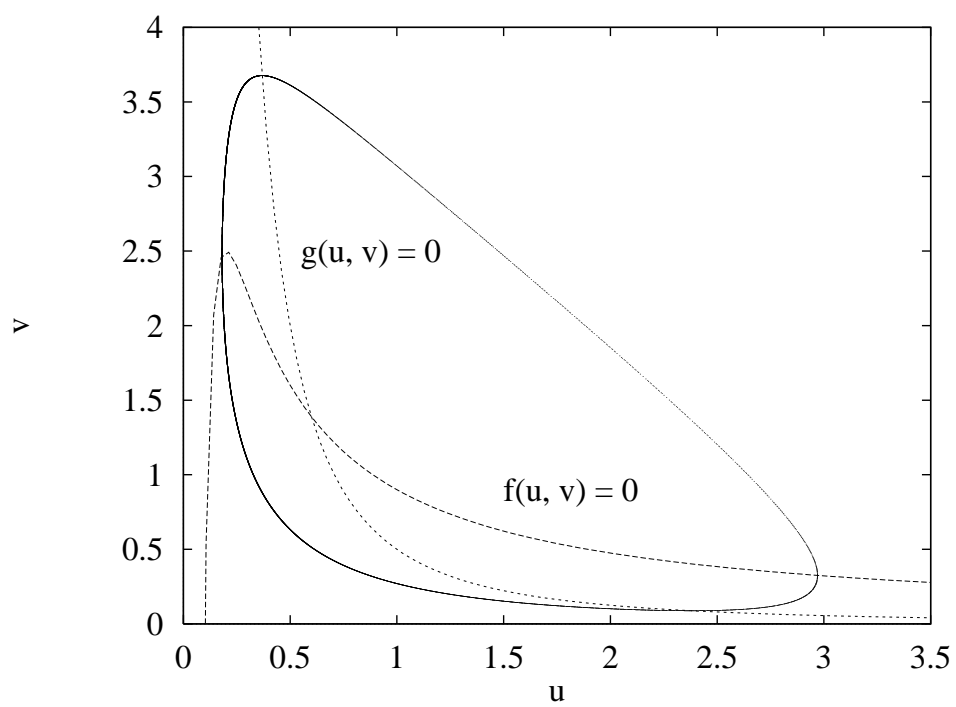


FIG. 1. The limit cycle of the Schnackenberg's tri-molecular two species model.

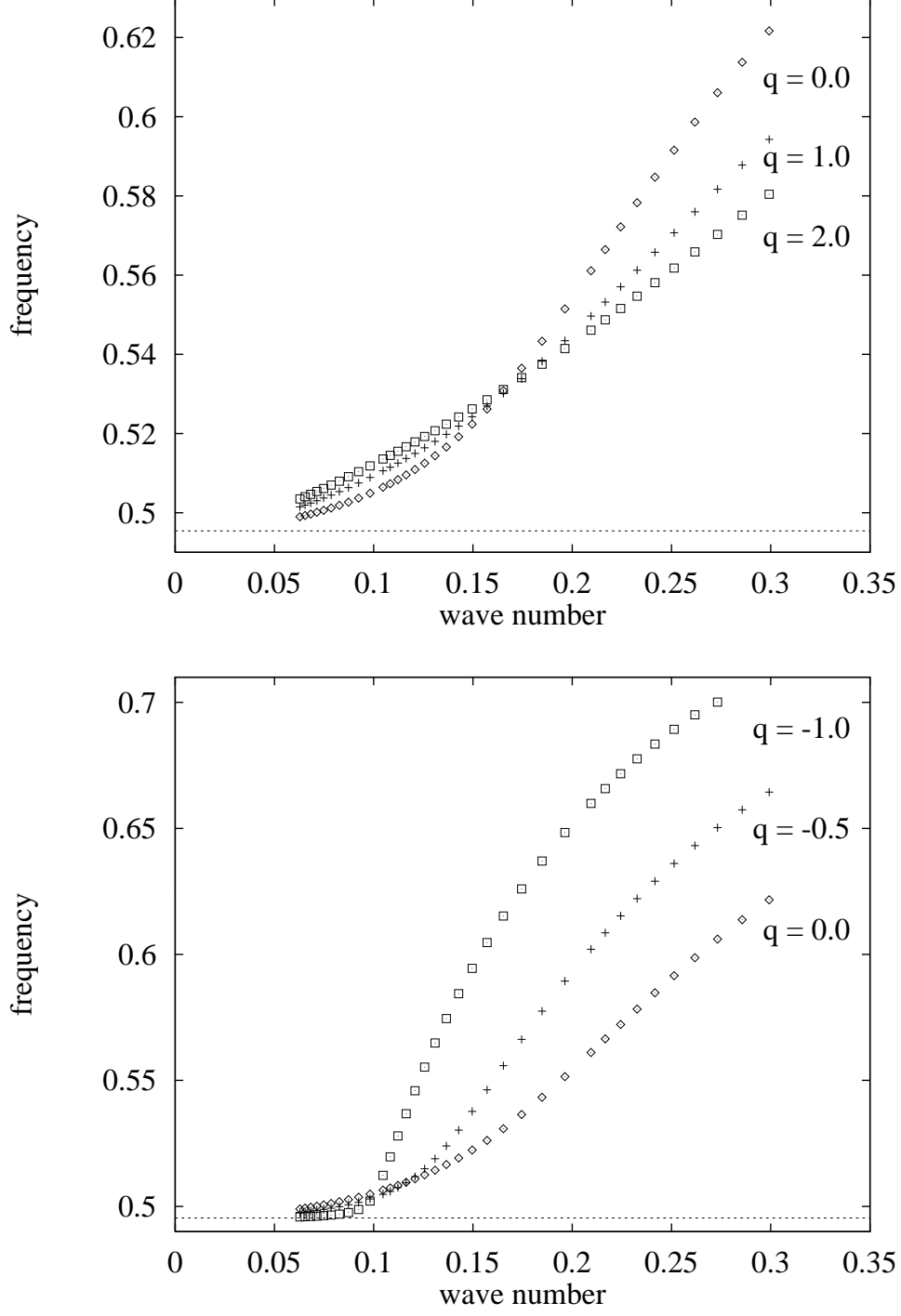


FIG. 2. Dispersion curves obtained by numerical calculations. The oscillation frequency  $\omega$  monotonically increase with the wave number  $k$ , and has the bulk frequency  $\omega_0 = 0.495$  in the limit of  $k \rightarrow 0$ .

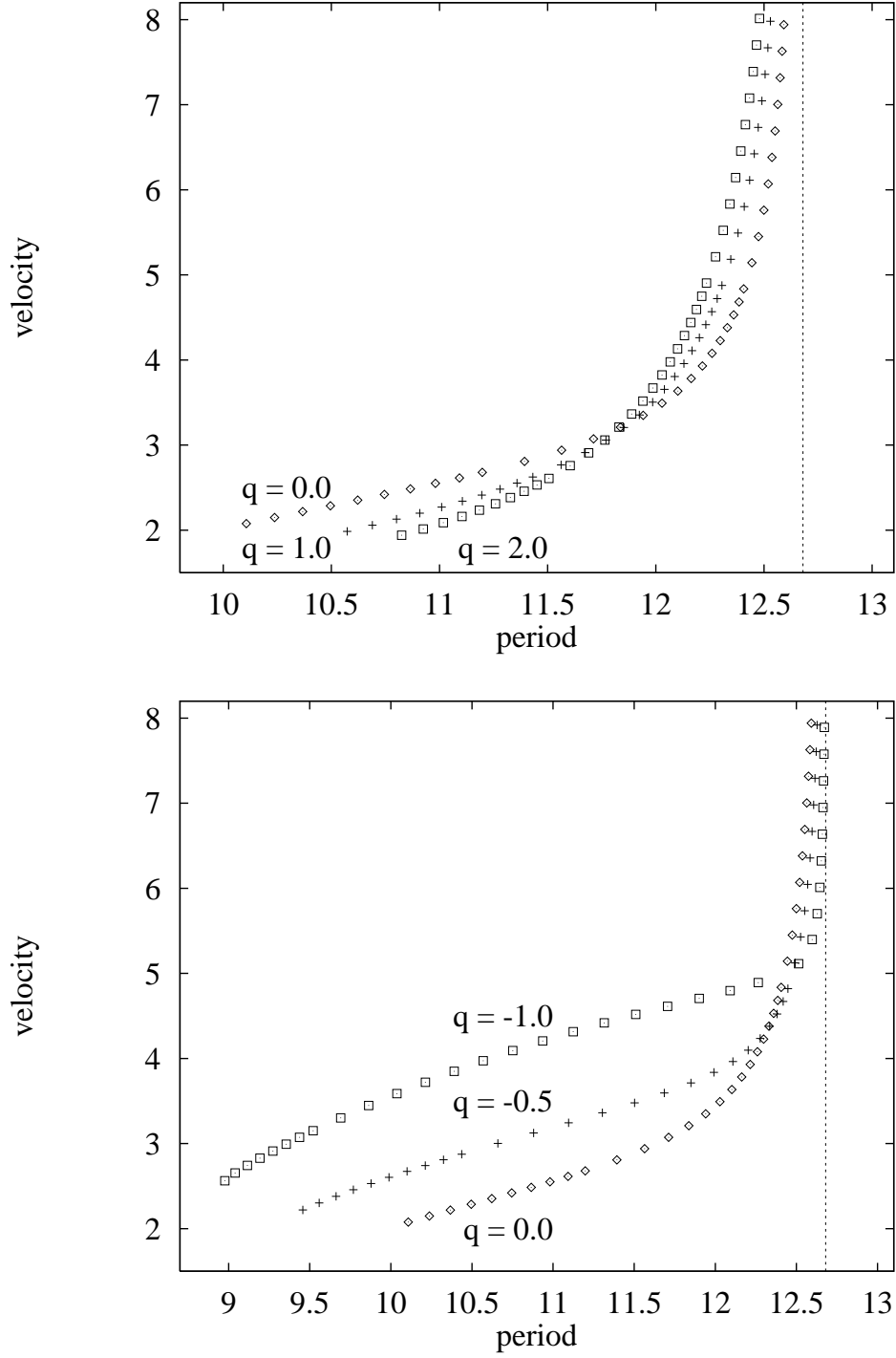


FIG. 3. The propagating velocity  $v$  is determined as the phase velocity  $\omega/k$ . The velocity becomes large and goes to infinity at the bulk period  $\tau_0 = 12.7$ . For negative value of  $q$ , the curves have large convex regions in period corresponding to trigger waves.